Negotiation between parents over care: reversible compensation during incubation

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Summary

Parental care is often beneficial for the young, but costly for the care-giving parent. Since both parents benefit from care via the offspring, whereas they pay the costs individually, a conflict is expected about how much care each parent should provide. How do parents settle this conflict? We addressed this question by reducing nest temperatures during incubation in the Kentish plover *Charadrius alexandrinus*, a small ground-nesting shorebird in which the parents share incubation. By cooling the clutch using a remote-controlled device built under the nest we experimentally increased the workload of either the male or the female in random order, and recorded the behavioral responses of the targeted parent and its mate. Unlike most previous manipulations of parental effort, our manipulation sought to measure a parent's response to an increase, not a shortfall, in the partner's contribution. The manipulation was also short-term and reversed between the members of a given pair. We found that there is a trade-off between the efforts of parents, since increased (or reduced) effort by the targeted parent was associated with decreased (or increased) effort by their mate, respectively. This result is consistent with theoretical models that predict compensation as a response to changed parental effort of the mate. We also found that compensation was consistent between treatments when the male or the female of a given pair was targeted. Furthermore, our results support the notion that parents adjust their effort in response to their mate's behavior in real time, i.e. they negotiate parental roles.

Keywords: sexual conflict, parental care, precocial bird, wader, shorebird

Short title: Parental negotiation during incubation

Introduction

Biparental care of young is an excellent model system for investigating cooperation and conflict between unrelated individuals. On the one hand, cooperation between parents is beneficial, since provisioning the eggs and young with nutrients, defending them from predators and training them in useful skills usually improve the offspring's chances of survival and reproduction (Clutton-Brock 1991, Balshine et al. 2002). On the other hand, parental care is costly since it takes time and energy, and the caring parent may be taken by predators (Lessells 1999, Houston et al. 2005). Finding the outcome of these conflicting selective forces is not straightforward, because the benefits are shared between the parents, i.e. via the offspring, whereas each parent pays the costs itself. The existence of biparental care in insects, fishes, frogs, birds and mammals thus provides excellent opportunities to test hypotheses about how conflict and cooperation influence social behavior (Trivers 1972, Parker et al. 2002).

How do parents settle their conflict? The influential model by Houston & Davies (1985) used provisioning rates of parents and predicted partial compensation; that is, if one parent increases its effort, the other parent should decrease its effort by a lesser extent. However, in Houston & Davies (1985) parents do not adjust their work rate in response to the behavior of their mate in real time, but their strategy is fixed in evolutionary time (a 'sealed bid' in game theoretic terminology). Models that incorporate repeated decisions of the parents ('negotiation') predict either compensation (McNamara et al. 1999), or responses ranging from compensation to matching, i.e. an increase in work rate in response to an increase by the mate (Taylor & Day 2004, Johnston & Hinde 2006).

69 Numerous experiments have been carried out to test the predictions of such models,
70 in birds, insects, fish and mammals. Two major approaches have been used to test the
71 responses of parents to changed effort by their mate: (i) mate removal (e.g. Erckmann
72 1983, Martin & Cooke 1987, Alatalo et al. 1988, Markman et al. 1996, Smiseth &
73 Amundsen 2000), and (ii) handicapping (attaching extra weights or clipping feathers,
74 e.g. Wright & Cuthill, 1989, Slagsvold & Lifjeld 1990, Markman et al. 1995, Sanz et al.
75 2000). The results of these experiments have been contradictory, since parents
76 responded variously to the changed work rate of their mate by compensation or
77 matching, whereas in some studies no significant response was detected (reviewed by
78 Bart & Tornes 1989, Sanz et al. 2000, Smiseth et al. 2005, Houston et al. 2005, Hinde
79 2006). These experiments, however, are limited in what can be deduced about the
80 negotiation process (if one exists), in that the manipulation usually lasted over several
81 days of the care period, and in each pair only a single parent was manipulated.
82 Here we investigate the responses of parents to changed effort by their partner in a
83 small shorebird (body mass: 40-44 g), the Kentish plover *Charadrius alexandrinus*, in
84 which the parents share incubation. The sexes have different incubation patterns: the
85 males incubate mostly during the night whereas females do most of the daylight
86 incubation (Rittinghaus 1961, Fraga & Amat 1996, Kosztolányi & Székely 2002). After
87 hatching of the chicks one parent (usually the female) may desert the brood, thus brood
88 care is variable in most populations: biparental, male-only and female-only care may all
89 occur in a single population (Lessells 1984, Warriner et al. 1986, Amat et al. 1999,
90 Kosztolányi et al. 2006).
91 To manipulate incubation effort in the Kentish plover we increased the workload of
92 parents by cooling the nest and the eggs using a remotely controlled device. Our

93 experiment is novel for two reasons. First, we used short-term manipulations (hours)
94 whereas previous studies of parental interactions employed long-lasting manipulations
95 (days, weeks; by removing the mate, or attaching extra weights or clipping feathers).
96 The advantage of our approach is that we can separate effects during and after
97 manipulations. Second, males and females of each pair were manipulated on different
98 days in random order, i.e. we reversed the manipulations between members of a given
99 pair. This has not been done in previous studies, except Hinde (2006) used playback of
100 begging calls to reversibly manipulate care by male and female great tits *Parus major*.
101 We had two major objectives. First, to test how parents respond to an increased
102 workload during incubation. Second, to test how males and females respond to a
103 changed level of parental effort of their mate. Unlike most avian studies of parental
104 effort, (i) we manipulated the parental behavior during incubation and not during brood
105 care, and (ii) we aimed to increase and not decrease the effort of the manipulated parent.
106 During incubation the costs of parental absence, and thus the joint commitment to care,
107 may differ from during chick feeding (e.g. prolonged absence may lead to embryo death
108 rather than retarded growth). An advantage of targeting incubation is that offspring
109 behavior during incubation is unlikely to confound the outcome of the negotiation
110 between the parents (Parker et al. 2002, Johnstone & Hinde 2006), since in behavioral
111 (though not evolutionary) terms an egg is a more passive player in the game than a
112 chick. A further difference between brood care and incubation in the context of parental
113 care is that during brood care the parents can independently increase the contribution to
114 chick feeding, whereas during incubation an increase in incubation time by one parent is
115 only possible if the other member of the pair is not sitting on, or can be persuaded to
116 leave, the nest.

Material and methods

Study area and field methods

The experiment was carried out at Al Wathba Wetland Reserve (24º 15.5' N, 54º 36.2' E) in the United Arab Emirates about 40 km south-east from Abu Dhabi, in two years: 2005 (23 March – 19 June) and 2006 (26 April – 12 July). The Reserve is 3.7 km long and 1.9 km wide, the total area is about 450 ha, and it is composed of natural and man-made water bodies with sand dunes separating the water bays of the lakes.

To study incubation behavior and manipulate the thermal condition of the nest an automatic nest monitoring system was developed (Figure 1). The system consisted of four main parts. First, an electronic balance (Navigator, Ohaus Corporation, Pine Brook, New Jersey, USA) was placed under the nest scrape and connected to a data logger (Gigalog, Audon Electronics, Nottingham, UK) to record the body mass of the incubating parent every 20 s. The nest was placed on a plastic tray on top of the balance. The extreme ambient temperature (see below) and strong wind, however, made the readings of the balance unreliable, so these measurements were not investigated further. Second, a thermo-probe was inserted into the bottom of the nest scrape, and another probe about 25 cm from the nest scrape at ground level to measure the thermal condition of the nest and the environment, respectively. The probes were connected to a data logger (Tinytag, Gemini Data Loggers Ltd., Chichester, UK) that recoded data every 20 s. Third, a small spy camera (Outdoorcam, Swann Communications Pty. Ltd., Richmond, Victoria, Australia) was positioned about 1 m from the nest and connected to a digital video recorder (MemoCam, Video Domain Technologies Ltd., Petah Tikva, Israel) to record the behavior of the parents every 20 s. The camera had infrared light

140 sources that allowed recording of behavior at night. The plumage of adult Kentish
141 plovers is sexually dimorphic during the breeding season and this allows identification
142 of sexes from the photos. Fourth, a Peltier heat pump (RS Components Ltd., Corby,
143 UK) was placed under the nest scrape to change the thermal condition of the nest. This
144 device was connected to a central unit that was remote controlled. The power was
145 supplied by a car battery. All parts of the system (except the camera) and the cables
146 were hidden underground to minimize the disturbance to the plovers.
147 The experiment lasted for four days at each nest. Before the experiment both
148 parents were captured, measured and color ringed. All experimental nests had three
149 eggs (modal clutch size), and the clutches were 11.9 ± 1.02 (mean ± SE, n = 20) days
150 old at the start of the experiment. On the first day the system was set up at the nest, the
151 second day was a baseline, and on the third and fourth days we cooled the nest between
152 either 22:00 – 04:00 or 05:00 – 09:00 to target the male or female, respectively (Figure
153 2). The order of cooling was randomized at a nest. The system was visited daily to
154 change memory cards in data loggers, to change the battery (every 2nd day), and to
155 check the system for proper operation. The mean length of these visits were 20.1 ± 0.56
156 min (mean ± SE, n = 20), and data from these periods were excluded from the analyses.
157 No visit was made during the manipulations (i.e. during cooling).
158 Data were collected by two nest monitoring systems at 20 nests in total. Three nests
159 were predated while the experiment was running, therefore data are missing for three
160 female manipulation days. At three different nests the parents delayed returning to the
161 nest after setting up the system; at these nests an extra baseline day was taken, and data
162 from the first baseline day were omitted.
163 We expected that the parents aim to mitigate the effect of cooling on egg

164 temperatures. To assess the effect of cooling on nest temperature without the parents,
165 we measured nest and ambient temperatures at five unused nests ('dummy nests'
166 henceforward; three nests in 2005 and two in 2006). In these cases the nest monitoring
167 system was set up at previously predated, abandoned or hatched Kentish plover nests
168 for one day, and three fresh eggs of Japanese quail *Coturnix japonica* were cooled for
169 equivalent periods for the male and female manipulation (22:00 – 04:00 or 05:00 –
170 09:00, respectively). The quail egg is similar in size and shape to the Kentish plover
171 egg.

172 ## Statistical analyses

173 We considered each nest as the unit of analysis. The effect of manipulation on
174 incubation behavior was measured by the change in incubation time (%, i.e. percentage
175 of incubation during manipulation day minus percentage of incubation during baseline
176 day). The baseline and manipulation days were divided into two parts: manipulation
177 period (22:00 – 04:00 and 05:00 – 09:00 for male and female manipulation day,
178 respectively), and after manipulation period (04:00 – 10:00 and 09:00 – 13:00 for male
179 and female manipulation day, respectively). The responses by the male and female
180 during and after manipulation were not influenced significantly by year, by the nest
181 monitoring system (set one or set two) used for data collection and manipulation, or by
182 the order of manipulation (ANOVAs, $p \geq 0.194$ in all cases), therefore these effects
183 were not considered in further analyses.
184 With the 22:00 – 04:00 manipulation period we targeted the male, whereas with the
185 05:00 – 09:00 period the female parent was targeted. However, the targeted parent did
186 not always incubate during the whole cooling period (see below); thus the amount of

187 manipulation experienced by a given parent depended on the time it spent on the nest
188 during manipulation. Therefore, we used a covariate (ΔT) in the linear models to
189 investigate the effect of manipulation on the response of the sexes. ΔT for a given sex
190 was defined as the absolute value of the effect of cooling on nest temperature (T_{nest}-
191 $T_{ambient}$) multiplied by the time the parent was incubating the nest during the cooling
192 period. The effect of cooling for a given day of the season was estimated by using the
193 temperature data of dummy nests (see below).
194 The presence of parents influenced the effect of cooling because the difference
195 between nest and ambient temperature (T_{nest}-$T_{ambient}$) was smaller at experimental nests
196 than at dummy nests (22:00 – 04:00, experimental nests: -1.2 ± 0.27 ºC, dummy nests: -
197 4.2 ± 0.52 ºC; t-test, $t_{23} = 4.924$, $p < 0.001$; 05:00 – 09:00, experimental nests: -
198 3.3 ± 0.25 ºC, dummy nests: -5.9 ± 0.32 ºC; $t_{20} = 5.245$, $p < 0.001$). Furthermore, the
199 effect of cooling (i.e. T_{nest}-$T_{ambient}$) at dummy nests tended to be larger in absolute value
200 over the breeding season (least-squares regressions, male manipulation: B = -
201 0.02 ± 0.021; $t_3 = 1.157$, $p = 0.331$; female manipulation: B = -0.02 ± 0.007; $t_3 = 3.552$,
202 $p = 0.038$). Therefore, the manipulations received by the sexes (ΔTs) were estimated
203 using temperature difference (T_{nest}-$T_{ambient}$) estimated for a given date using the
204 coefficients of the above least-squares regressions.
205 During male-targeted manipulations the male was on the nest 70.2 ± 5.06% of the
206 time (mean ± SE), the female 26.2 ± 4.71%, and neither parent 3.6 ± 0.71%. That is,
207 males spent more time on the nest than females when males were targeted (paired t-test,
208 $t_{19} = 4.522$, $p < 0.001$). In contrast, during female-targeted manipulations the females
209 spent more time on the nest than males ($t_{16} = 11.525$, $p < 0.001$; male: 9.1 ± 2.84%,
210 female: 77.3 ± 3.41%, neither: 13.6 ± 2.10%). Thus, during male-targeted manipulations

211 the males experienced more cooling than females (ΔT_{male} = 17.5 ± 1.34 ºC × h,
212 ΔT_{female} = 6.8 ± 1.28 ºC × h; paired t-test, t_{19} = 4.321, p<0.001), whereas during female-
213 targeted manipulations females experienced more cooling than males
214 (ΔT_{male} = 2.1 ± 0.69 ºC × h, ΔT_{female} = 18.2 ± 0.94 ºC × h; t_{16} = 10.694, p < 0.001). This
215 is, of course, what the experiment was designed to achieve, but we stress that 'male'
216 and 'female' targeting was a statistical, not deterministic, difference because sometimes
217 the 'wrong' sex was present and experienced the manipulation targeted at its mate.
218 One may argue that the responses of parents may depend on their original effort; for
219 instance, if a parent is already incubating 90% of its time, it is less likely to increase its
220 incubation as a response to manipulation than a parent that incubates only 10% of its
221 time (a 'ceiling effect'). We investigated this proposition by weighting the response as
222 exp(x/100) when x, i.e. the change in incubation time was a positive response, and
223 exp(1-x/100) when x was negative. However, applying weights does not change our
224 conclusions, so these results are not reported.
225 We used vectors to analyze the responses of parents to their mate's behavior. The
226 baseline period was taken as the origin, and the coordinates represented changes in male
227 and female incubation compared to the baseline period. Thus, a vector captured the joint
228 change in the level of incubation of the male and female in a given pair. In one pair
229 incubation did not change during the male manipulation period compared to the
230 baseline (i.e. the length of the vector was zero), therefore this nest was not considered
231 during the male manipulation period.
232 To investigate the distribution of vectors, we divided the parameter space into two
233 triangles along the male change = female change (+1 slope) line (isocline,
234 henceforward). Vectors between 0º and 45º either side of the isocline mean that both

parents increased incubation ('matching', see Figure 3), vectors between 45º and 135º mean that one parent increased incubation while the other decreased ('compensation' by the female or the male; upper left and lower right triangles, respectively), whereas vectors between 135º and 180º mean that both parents decreased incubation ('negative matching').

We investigated the behavioral responses in vector space in three ways. First, we used the absolute deviation of vectors from the isocline, and calculated the mean deviation and their 95% confidence intervals (95% CI). Second, we also considered the length of the vectors and calculated the mean vector and the 95% confidence area for the altered level of incubation separately for the two triangles. Finally, to compare the responses of pairs between male and female manipulations we used the absolute deviation of vectors from the isocline.

Statistical analyses were carried out using R 2.6.0 (R Development Core Team 2007). Values are given as mean ± SE unless indicated otherwise.

Results

Effect of manipulation on incubation behavior

Cooling of the eggs influenced parental behavior: total incubation was higher during male manipulation than during baseline periods, and total incubation increased with the cooling the parents experienced (Table 1). Males, but not females, increased their incubation time with the manipulation they received (regression on ΔT). After manipulation, male incubation non-significantly tended to decrease, whereas female incubation increased compared to the baseline day (Table 1). Similar to the preceding

257 results, total incubation was higher during female manipulation than during baseline
258 (Table 1). Furthermore, incubation by females, but not males, was higher during the
259 manipulation than baseline (Table 1). After female manipulation, total incubation was
260 significantly higher in nests that had previously received more cooling (regression on
261 ΔT), but no other relationships after female manipulation were significant (Table 1).
262 The non-significant trend was for females to decrease incubation, and for males to
263 increase, after female manipulation.

264 Whilst these results show that the manipulation had an effect on parental behavior,
265 they cannot explain how a parent responded to the changed effort of its mate, because
266 here males and females were tested independently. Furthermore, the slopes on ΔT are
267 not comparable between the sexes because the ranges of the explanatory variable (i.e.
268 the amount of manipulation received) were different between males and females (see
269 Methods for the mean ΔT received by the sexes).

270 Response to mate's behavior

271 Compensation by the mate, rather than matching, was the most common response to the
272 manipulation. Firstly, during male manipulations the mean angle of vectors from the
273 isocline and their 95% confidence interval fell into the compensation area (mean: 68.3º,
274 95% CI: 57.0º – 79.6º, $n = 19$). Similarly, the mean vectors and their confidence areas
275 were restricted (upper left triangle) or almost restricted (lower right triangle) to the
276 compensation areas (Figure 3). Unexpectedly, in nine out of 19 nests, the female
277 increased her incubation (and the male showed compensatory decrease) when the male
278 was the intended target. We investigated why this might have happened. It turned out
279 that at these nine nests the females experienced significantly more cooling

($\Delta T_{prop} = \Delta T_{female} \times (\Delta T_{male} + \Delta T_{female})^{-1} = 0.41 \pm 0.060$), than at the other ten nests ($\Delta T_{prop} = 0.18 \pm 0.063$; t-test, $t_{17} = 2.579$, $p = 0.019$).

Secondly, the effects of female manipulations were consistent with that of the male manipulations (mean angle: 70.2º, 95% CI: 56.8º – 83.7º, $n = 17$), and the mean vectors and their confidence areas were nearly always in the compensation areas (Figure 3).

Thirdly, after manipulations the responses of the parents with respect to each other were similar to the ones during manipulations, because the mean angle of vectors were inside the compensation areas (male manipulation, mean: 85.7º, 95% CI: 64.9º – 106.5º, $n = 20$; female manipulation, mean: 90.4º, 95% CI: 76.9º – 103.9º, $n = 17$). Furthermore, both the mean vectors and their confidence areas were largely restricted to the compensation areas (Figure 3).

It is unlikely that the compensatory responses were due to an upper limit in total incubation, because the percentage of time the two parents spent on the nest was significantly different from 100% during the manipulation and after manipulation periods on both manipulation days (during male manipulation: 96.4 ± 0.71%, $t_{19} = 5.052$, $p < 0.001$; after male manipulation: 85.5 ± 1.68%, $t_{19} = 8.626$, $p < 0.001$; during female manipulation: 86.4 ± 2.10%, $t_{16} = 6.471$, $p < 0.001$; after female manipulation: 94.0 ± 1.99%, $t_{16} = 3.039$, $p = 0.008$, see also Methods for a summary of ceiling effect analyses).

Consistency of responses

Finally, the responses of parents were highly consistent between male and female manipulations (Figure 4, $n = 13$ pairs out of 16 were in, or on the border of, the compensation area, i.e. within 25% of the whole parameter space; binomial test using

303 $P = 0.25$, $p < 0.001$), and after manipulations ($n = 11$ pairs out of 17; $p = 0.001$).

304 # Discussion

305 Our experiment provided three key results. First, Kentish plover parents responded to
306 the changed level of incubation of their partner in real time, a result consistent with
307 negotiating parental roles (*sensu* McNamara et al. 1999). Thus our results of the
308 manipulation of parental workload during incubation are in line with the results of most
309 experimental manipulations of parental effort during brood rearing of birds. Most
310 studies have also found real-time responses to the change in parental effort by the mate
311 (e.g. Wright & Cuthill 1989, Markman et al. 1995, Sanz et al. 2000), whereas few have
312 supported the 'sealed bid' notion (Schwagmeyer et al. 2002 and references therein). The
313 reason for these intriguing interspecific differences in negotiation strategies remains
314 unknown.

315 Second, we showed that compensation, rather than matching, was the most
316 common response by Kentish plover parents to cooling of the eggs (or the partner's
317 response to cooling). That is, our results are in line with theoretical models that predict
318 compensation between parents (McNamara et al. 1999, Johnstone & Hinde 2006).
319 Unlike most previous experimental manipulations of parental effort, our manipulations
320 aimed at increasing the contribution of the targeted parents (*cf*. handicapping and
321 removal), and we did achieve this because total incubation increased during both
322 manipulation periods compared to the baseline day. When one parent increased its
323 incubation time in response to egg cooling, the response of the partner was usually not
324 to keep its own effort constant, or match it, but to decrease it. The latter result suggests
325 that there is a conflict between the parents over the amount of parental effort, and that

each parent tries to avoid the costs of parental care and shunt the work on its partner (Houston et al. 2005). Some of our results indicate overcompensation (e.g. increasing total incubation). These results are intriguing because they are not in line with the results of most previous experiments and the predictions of theoretical models. However, our results are not comparable to previous studies because we aimed at increasing the effort of the manipulated parents.

Third, the parents' responses were consistent during the manipulation and after manipulation periods, since most pairs exhibited compensation during all four periods. This consistency strengthens the suggestion that the actual changes in parental effort are results of a negotiation process.

To our knowledge, the only experimental study on parental effort that, similarly to our study, has aimed at increasing the contribution of the targeted parent was Hinde (2006). Using playback of begging calls to modulate feeding rates in great tit, she showed matching rather than compensation between parents. The reason for these contrasting results may lie in the differences in information available for the parents, since the information the parents have on the need or value of offspring may profoundly influence whether compensation or matching is the outcome of the negotiation process (Johnstone & Hinde 2006). Our results are in line with the predictions of Johnstone & Hinde (2006), because compensation is expected if the parents have reliable and symmetric information about the need of the offspring, which in the Kentish plover may be the difference between the optimal and actual egg temperature. In contrast, in Hinde (2006) the great tit parents may have used the mate's increased work rate as a cue of increased brood need or quality, and they responded by matching, as predicted by Johnstone & Hinde (2006) if the parents have only partial information regarding brood

need and quality.

The trade-off between male and female parental effort observed in this study has also been seen in comparative studies. Olson et al. (2008) showed, using parental care data from 193 bird species, a negative relationship between male and female care (see Thomas et al. 2007 for a similar result in shorebirds). These results are consistent with the proposition that there is an evolutionary tug-of-war between the sexes over who should care for the young and, although there is no necessary relationship between evolutionary and behavioral responses, this conflict may also be manifested during real-time behavioral decisions.

In conclusion, we have shown that parents rapidly and consistently respond to the changed effort of their mate in a ground-nesting shorebird, the Kentish plover, during incubation. We have also shown a trade-off between the parental effort by males and females (compensation). However, we do not know the limits of the compensatory response. That is, how far the pairs can be moved from their negotiated effort before failing to compensate and, for example, deserting the nest. To reveal the stability of the compensatory response, repeated manipulations of the same individuals with different levels of manipulations (e.g. variable amount of cooling) is needed.

Funding

The study was funded by a BBSRC grant (BBS/B/05788 to TS, ICC, A. I. Houston, and J. M. McNamara) and by Environment Agency – Abu Dhabi (EAD). AK was also supported by a Magyary Postdoctoral Fellowship.

We are grateful to Steve Routley for his help in designing and preparing the nest

373 monitoring system. Peter Hellyer and the EAD staff, especially Salim Javed and Shahid
374 Khan, gave logistic help during fieldwork. We thank for the assistance of Clemens
375 Küpper, Thijs van Overveld and David Jansen in the field, and Monif Al-Rashidi in
376 analyzing photos. The fieldwork was licensed by EAD, and we followed the
377 ABS/ASAB Guidelines for the Treatment of Animals in Behavioral Research and
378 Teaching.

379 # References

380 Alatalo RV, Gottlander K, Lundberg A. 1988. Conflict or cooperation between parents
381 in feeding nestlings in the pied flycatcher *Ficedula hypoleuca*. Ornis Scand.
382 19:31–34.
383 Amat JA, Fraga RM, Arroyo GM. 1999. Brood desertion and polygamous breeding in
384 the Kentish plover *Charadrius alexandrinus*. Ibis. 141:596–607.
385 Balshine S, Kempenaers B, Székely T. 2002. Conflict and cooperation in parental care –
386 Introduction. Phil Trans R Soc Lond B. 357:237–240.
387 Bart J, Tornes A. 1989. Importance of monogamous male birds in determining
388 reproductive success. Behav Ecol and Sociobiol. 24:109-116.
389 Clutton-Brock TH. 1991. The Evolution of Parental Care. Princeton: Princeton
390 University Press.
391 Erckmann WJ. 1983. The evolution of polyandry in shorebirds: An evaluation of
392 hypotheses, In: Wasser SK, editor. Social Behavior of Female Vertebrates. New
393 York: Academic Press. p. 113–168.
394 Fraga RM, Amat JA. 1996. Breeding biology of a Kentish plover (*Charadrius*
395 *alexandrinus*) population in an inland saline lake. Ardeola. 43:69–85.

396 Hinde CA. 2006. Negotiation over offspring care? A positive response to partner-
397 provisioning rate in great tits. Behav Ecol. 17:6–12.
398 Houston AI, Davies NB. 1985. The evolution of cooperation and life history in the
399 dunnock, *Prunella modularis*. In: Sibly RM, Smith RH, editors. Behavioural
400 ecolgy: ecological consequences of adaptive behaviour. Oxford: Blackwell
401 Scientific Publications. p. 471–487.
402 Houston AI, Székely T, McNamara JM. 2005. Conflict over parental care. Trends Ecol
403 Evol. 20:33–38.
404 Johnstone RA, Hinde CA. 2006. Negotiation over offspring care – how should parents
405 respond to each other's efforts? Behav Ecol. 17:818–827.
406 Kosztolányi A, Székely T. 2002. Using a transponder system to monitor incubation
407 routines of snowy plovers. J Field Ornith. 73:199–205.
408 Kosztolányi A, Székely T, Cuthill IC, Yılmaz KT, Berberoğlu S. 2006. Ecological
409 constraints on breeding system evolution: the influence of habitat on brood
410 desertion in Kentish plover. J Anim Ecol. 75:257–265.
411 Lessells CM. 1984. The mating system of Kentish plovers *Charadrius alexandrinus*.
412 Ibis. 126:474–483.
413 Lessells CM. 1999. Sexual conflict in animals. In: Keller L, editor. Levels of Selection
414 in Evolution. Princeton: Princeton University Press. p. 75–99.
415 Markman S, Yom-Tov Y, Wright J. 1995. Male parental care in the orange-tufted
416 sunbird: behavioural adjustments in provisioning and nest guarding effort. Anim
417 Behav. 50:655–669.
418 Markman S, Yom-Tov Y, Wright J. 1996. The effect of male removal on female
419 parental care in the orange-tufted sunbird. Anim Behav. 52:437–444.

Martin K, Cooke F. 1987. Bi-parental care in willow ptarmigan: a luxury? Anim Behav. 35:369–379.

McNamara JM, Gasson CE, Houston AI. 1999. Incorporating rules for responding into evolutionary games. Nature. 401:368–371.

Olson VA, Liker A, Freckleton RP, Székely T. 2008. Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. Proc Roy Soc B. 275:301–307.

Parker G, Royle NJ, Hartley IR. 2002. Intrafamilial conflict and parental investment: a synthesis. Phil Trans R Soc B. 357:295–307.

Rittinghaus H. 1961. *Der Seeregenpfeifer(Charadrius alexandrinus L.)*. Wittenberg, Lutherstadt: A. Ziemsen Verlag.

Sanz JJ, Kranenbarg S, Tinbergen JM. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). J Anim Ecol. 69:74–84.

Schwagmeyer P, Mock DW, Parker GA. 2002. Biparental care in house sparrows: negotiation or sealed bid? Behav Ecol. 13:713–721.

Slagsvold T, Lifjeld JT. 1990. Influence of male and female quality on clutch size in tits (*Parus spp.*). Ecology. 71:1258–1266.

Smiseth PT, Amundsen T. 2000. Does female plumage coloration signal parental quality? A male removal experiment with the bluethroat (*Luscinia s. svecica*). Behav Ecol and Sociobiol. 47:205–212.

Smiseth PT, Dawson C, Varley E, Moore AJ. 2005. How do caring parents respond to mate loss? Differential response by males and females. Anim Behav. 69:551–559.

Taylor PD, Day T. 2004. Stability in negotiation games and the emergence of

444 cooperation. Proc Roy Soc B. 271:669–674.
445 Thomas GH, Székely T, Reynolds JD. 2007. Sexual conflict and the evolution of
446 breeding systems in shorebirds. Adv Study Behav. 37:279–342.
447 Trivers R. 1972. Parental investment and sexual selection. In: Campbell B, editor.
448 Sexual Selection and the Descent of Man. Chicago: Aldine Press. p. 136–179.
449 Warriner JS, Warriner JC, Page GW, Stenzel LE. 1986. Mating system and reproductive
450 success of a small population of polygamous snowy plovers. Wilson Bull. 98:15–
451 37.
452 Wright J, Cuthill IC. 1989. Manipulation of sex differences in parental care. Behav Ecol
453 and Sociobiol. 25:171–181.
454

Figure legends

Figure 1

The system we used for monitoring and manipulating nest temperatures in the field. (a) The camera with a Kentish plover nest, (b) the electronic balance, datalogger and Tinytag temperature logger, (c) the video recorder, the main unit (controlling the Peltier device and distributing power), and the battery in a separate box about 5 m from the nest.

Figure 2

The effects of cooling on internal nest temperature (solid line) and the ambient ground temperature (broken line) at an experimental nest. In this example the first cooling targeted the male, and the second cooling the female.

Figure 3

The responses of Kentish plover parents during manipulation (left panels) and after manipulation (right panels). The thick vectors are the mean of vectors in the upper left and lower right triangles, and the shaded boxes are the 95% confidence areas for the mean vectors. The number of nests (*n*) is given for each triangle (see Methods).

Figure 4

Summary of parental responses. Angles are given as the absolute deviation from the isocline (see Methods). The behaviors of a pair during manipulation (●) and after manipulation (○) are connected.

Table 1

Change in incubation time (%, manipulation − baseline) in Kentish plover parents, and the effect of received manipulation (ΔT, ºC × h) on the change in incubation time expressed as the slope of least-squares regressions. ΔT_{sex} means manipulation received by the male, the female and by both sexes, respectively.

	Change in incubation	**Slope on ΔT_{sex}**
Male manipulation		
During manipulation (22:00 – 04:00)		
Male	3.3 ± 4.80, $p = 0.498$	**1.9 ± 0.71, $p = 0.014$**
Female	1.9 ± 4.36, $p = 0.671$	1.3 ± 0.74, $p = 0.104$
Total	**5.2 ± 1.79, $p = 0.009$**	**1.1 ± 0.43, $p = 0.026$**
After manipulation (04:00 – 10:00)		
Male	-5.1 ± 2.66, $p = 0.070$	0.5 ± 0.46, $p = 0.317$
Female	**11.4 ± 4.09, $p = 0.011$**	-1.1 ± 0.70, $p = 0.126$
Total	6.3 ± 3.67, $p = 0.100$	0.4 ± 1.02, $p = 0.731$
Female manipulation		
During manipulation (05:00 – 09:00)		
Male	-4.0 ± 2.49, $p = 0.131$	-0.3 ± 0.93, $p = 0.723$
Female	**19.3 ± 6.42, $p = 0.008$**	2.6 ± 1.62, $p = 0.122$
Total	**15.4 ± 5.74, $p = 0.017$**	3.5 ± 1.94, $p = 0.093$
After manipulation (09:00 – 13:00)		
Male	0.6 ± 3.42, $p = 0.859$	-0.8 ± 1.26, $p = 0.514$
Female	-1.7 ± 3.06, $p = 0.584$	-0.4 ± 0.83, $p = 0.613$
Total	-1.1 ± 1.50, $p = 0.475$	**1.1 ± 0.48, $p = 0.037$**

Means ± SEs, and probabilities from one-sample t-tests on the change in incubation ($df = 19$ and $df = 16$ for male and female manipulation, respectively), and on the slope of least-squares regressions ($df = 18$ and $df = 15$ for male and female manipulation, respectively) are given. Statistically significant values are in bold.